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R. L. Blackman

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Biological approaches to the control of aphids

By R. L. Blackman

British Museum (Natural History), London, SW7 5BD

In the context of the International Biological Programme, the term *biological control* is used in its widest sense, to include any method which utilizes particular features of the biology of a pest species in order to limit its numbers, or the damage it causes. United Kingdom work has centred on aphids, a group which includes some of the most important world-wide pests of crops. With one particularly cosmopolitan and damaging species (*Myzus persicae*) as a model, the aims have been to highlight the problems which are peculiar to aphids and to provide a basis from which to work towards ecologically sound control methods. This paper reviews recent studies in the United Kingdom on four important aspects of aphid biology, namely genetic variation, host plant relations, population dynamics and dispersal by flight, and discusses future strategies for aphid control in the light of this work.

Introduction

The International Biological Programme core project on Biological Control comprises five sub-projects concerned with the control of five groups of arthropod pests: rice stem-borers, spider mites, scale insects, fruit flies and aphids. Biological control of the red spider mite *Tetranychus urticae* Koch on glasshouse cucumbers was pioneered at the Glasshouse Crops Research Institute by N. W. Hussey and colleagues, and Hussey has acted as international coordinator for the spider mite project. However, United Kingdom I.B.P.-sponsored work has been almost entirely concerned with aphids. There are good reasons for this. Aphids, taken as a group, are among the most important pests of crops in the world, especially in temperate regions. In Britain their importance is reflected in the fact that all government and government-aided agricultural research institutes have for many years been actively engaged in research into aphid biology and control. In addition, there already existed in universities in the United Kingdom, at the outset of the I.B.P., a number of research schools in applied aphid biology receiving funds from grant-awarding bodies such as the Research Councils. It was thus logical if not inevitable that a nationally-funded United Kingdom contribution to the I.B.P. should build on foundations already laid and make use of the technical expertise already available by concentrating on the study of aphids.

The first meeting of an international working group to formulate the objectives of the aphid project was held at Imperial College Field Station, Silwood Park, in April 1967 under the chairmanship of M. J. Way. A principal decision reached at this meeting was to orientate the project around a single species, which in this country is commonly referred to as the peach-potato aphid, *Myzus persicae* (Sulzer). *M. persicae* is probably the aphid species with greatest world-wide importance. This one species presents a major problem in the growing of peaches, potatoes, brassica crops, sugar beet, tobacco, egg-plants and peppers, to name but a few of its economically important host plants, in every part of the world where these crops are grown. The principal damage done by *M. persicae* to many crops is indirect, as this aphid is a very

efficient vector of plant virus diseases. Insects which carry plant viruses present especially difficult control problems, because they are damaging at low population densities. This is particularly true of aphids, which have a highly dispersive type of host-finding behaviour. Consider, for example, a single winged female of *M. persicae* arriving in a potato field with salivary glands full of potato leaf-roll virus. It will alight and probe the tissues of one plant after another before finally either settling to feed and reproduce or flying off elsewhere. Thus each aphid acts as a miniature flying syringe inoculating numerous plants and spreading disease through the crop.

How can we prevent this happening? Chemical control can only be effective when carefully timed, and may fail if the aphid develops resistance. For over ten years the incidence of virus yellows in sugar beet in England was held at a low level by a control programme that included an effective early warning scheme (Hull 1974), which told growers when to spray their crops so as to prevent spread of disease from the initial foci of aphid infestation. In 1974, however, yellows incidence soared, apparently because of a combination of factors which included the development of significant levels of resistance to organophosphorus insecticide in *M. persicae* (Needham & Devonshire 1975). Conventional biological control relying on natural enemies in the crop environment is not a feasible alternative to chemicals, because biological control agents take time to act and can hardly be very effective in a situation where the principal damage may be done during the initial colonization of the crop by flying aphids. One possibility is that we can find a method to reduce the numbers of winged aphids arriving on the crop. This requires knowledge of the biology and ecology of the aphid on its alternative host plants, even assuming we know where the immigrants are coming from. Perhaps we can breed or otherwise induce a degree of resistance or tolerance to aphids and the virus diseases they carry into the crops we grow. Such an approach may require a wealth of information about the physiological relations between the aphid and its host plants, and about the genetical potentialities of the aphid to adapt to the new crop varieties. One day we might even find ways of tinkering with the genetic constitution of the aphids themselves so as to render them harmless. But for the foreseeable future, any really effective control of aphids such as *M. persicae* will have to include some use of chemical insecticides. These chemicals and their application will require a more sophisticated approach than has been generally the case hitherto. The insecticides will have to kill aphids selectively and leave their natural enemies relatively unharmed. A range of these selective aphid-killers will be required to overcome the resistance problem. The precise timing of applications will be dependant on accurate information about the movements of the aphids and the dates of their arrival on the crop. Again, the conclusion is reached that any short or long term answer to the problems of aphid control is likely to depend for its success on pertinent biological information about the aphids themselves.

It could be asked why the great volume of research already published on aphids does not include this information. Ecological and genetical studies of aphids present a great many difficulties even if the field of study were limited to a particular aphid-hostplant association chosen for its simplicity. The principal pest species, however, almost without exception have highly complex ecological relationships. *M. persicae* is the supreme example of this. It is such an important pest because of its extreme polyphagy, its highly dispersive behaviour and its genetical variability (and hence adaptability): the very factors which make it such an unsuitable subject for ecological and genetic study. The review by van Emden, Eastop, Hughes & Way (1969) of the ecology of *M. persicae*, with 647 references, underlines the important gaps in our knowledge of this one species. By choosing *M. persicae* as a model for the International Biological

Programme project, the working group were really 'jumping in at the deep end' of applied aphid ecology. Nevertheless it was felt that this species, as a truly international pest insect, was an obvious candidate for I.B.P. work. The aims of the aphid project were not to devise a detailed scheme for controlling *M. persicae*. In fact, control of *M. persicae* cannot be accomplished by one general scheme; each crop and each situation are likely to require individual consideration. Rather it was hoped to make a coordinated effort to increase knowledge of aphid biology in all areas relevant to the improvement of control measures. It seemed probable that by concentrating this effort on and around *M. persicae*, the project would cover all the major problems of applied aphid biology.

Inherent variation

It is logical to start by defining our subject matter. What is *Myzus persicae*? If we call *M. persicae* a species, using the term species in the conventional sense as a group of interbreeding individuals, then we certainly do not have an adequate answer to this question. The taxonomic status of *M. persicae* is considered by van Emden *et al.* (1969). In an aphid which is as polyphagous and cosmopolitan as *M. persicae* one would expect to find considerable intraspecific variation. Apparently distinct intraspecific variants have been given the status of subspecies by some taxonomists, usually where there is evidence of interruption of gene flow. But the term most extensively used by non-taxonomists has been 'biotype'. The uses and abuses of the 'biotype concept' are discussed by Eastop (1973a). The essential point is that the 'biotype' is a terminological convenience, meaning no more than a collection of individuals within one species which have one character in particular in common. Usually this is a character which is of special interest to the research worker such as virus-transmitting ability, host-plant preference or insecticidal resistance. To call a group of individuals a biotype says nothing about the relations between individuals within the group nor between the group in question and other groups, nor does it imply any degree of permanence or predictability. Often 'biotype' will be synonymous with 'clone', and indeed, as the parthenogenetically derived populations of an aphid each summer consist of an indefinite number of temporarily isolated clones, the number of biotypes one could describe if one wanted to engage in a totally unprofitable occupation would be limitless. The important thing is to recognize the limitations of the term biotype, and to seek to establish the genetic basis for any observed common biological property of a group of aphids, for only then can the results of an investigation have a clear predictive value.

An example is provided by the life cycle of *M. persicae*. The annual life history of *M. persicae* follows two pathways, a sexual one and a parthenogenetic one. In colder climates, for example in Central Europe, all populations in the field produce sexual forms in autumn in the well-known aphid fashion by responding to the reduced daylength, and winter is passed as a fertilized egg on the primary host, usually the peach tree *Prunus persica* Stokes. In tropical climates, *M. persicae* reproduces by year-round parthenogenesis on secondary herbaceous host plants. In the United Kingdom and in many other parts of the world with mild temperate winters, *M. persicae* maintains alternative methods of overwintering. Only a proportion of the population enters the sexual phase. The remainder continues to reproduce by parthenogenesis, and some aphids manage to survive the winter, provided that conditions do not become too severe, to build up their populations again the following spring. The crucial question is, are the two pathways genetically isolated from one another, in which case one might expect to find that

one could split the species into two biologically meaningful entities, based on the life cycle differences? Alternatively, is there some connection between the two overwintering pathways, and if so, how is life cycle variation maintained in the one species from year to year?

The key to the problem lies in the photoperiodic response of the aphids, the mechanism which triggers the production of sexual forms. At Imperial College, Blackman (1971 a) established clones from individual parthenogenetic females collected on summer host plants, and then examined the variation in the response of these clones to artificial short days. It was found that discrete differences in photoperiodic response existed within populations, and clones could be classified according to whether they were terminated by production of oviparae and males (*holocyclic*), continued parthenogenetic reproduction but produced some males (*androcyclic*), or failed to produce any sexual morphs at all in response to short photoperiod (*anholocyclic*) (figure 1). These differences were unaffected by changes of host plant, or of temperature or photoperiod below the critical level for the response, and were clearly determined genetically. In fact, strictly anholocyclic clones with no response at all to short days were rather rare, the androcyclic form of response being most common in British *M. persicae*.
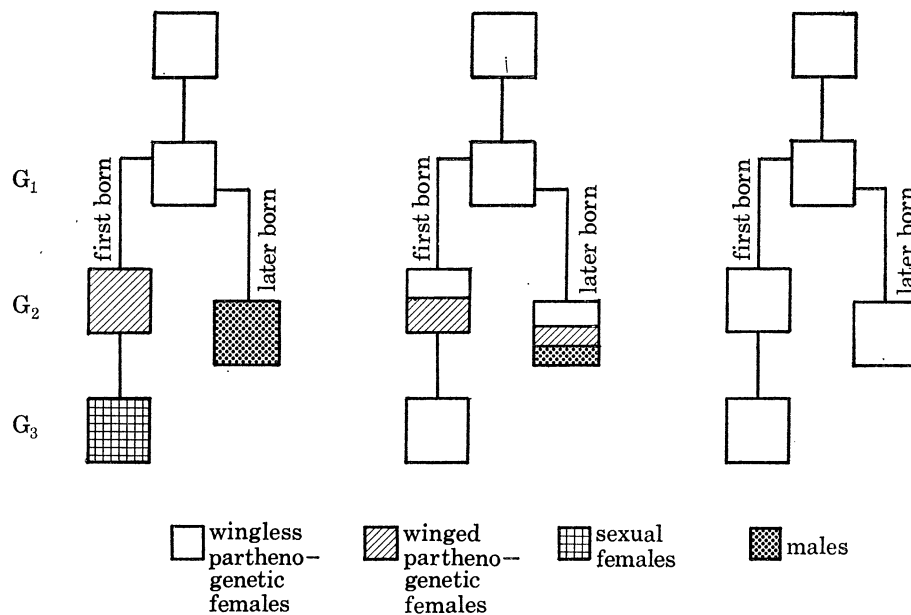

FIGURE 1. The three main types of response to short photoperiod in *Myzus persicae*. G_1, G_2 and G_3 are successive generations after transfer to the short day conditions.

Studies of the inheritance of the life cycle traits were initiated by crossing sexual females of a holocyclic clone with males of an androcyclic clone (Blackman 1972). These studies were continued for four successive sexual generations, and the results strongly support the hypothesis that the androcyclic trait is determined monofactorially and is recessive to holocycly. Androcycly can thus be inherited through the sexual phase, so that after a severe winter genotypes with the ability to overwinter parthenogenetically will be generated afresh by the breeding system (figure 2). It seems that some kind of genetic polymorphism is involved in the maintenance of life cycle variation in *M. persicae*, although how this is stabilized is still obscure.

An attempt was made (Blackman 1974) to explain the world-wide pattern of life cycle variation in *M. persicae* in terms of temperature differences between regions, assuming that the

photoperiodic response is geared to local conditions. Much of the information used was obtained by sending out a questionnaire to aphid specialists in all parts of the world (Blackman 1975). This was a speculative exercise based for the most part on inadequate information, but it may help to stimulate the further research which is badly needed.
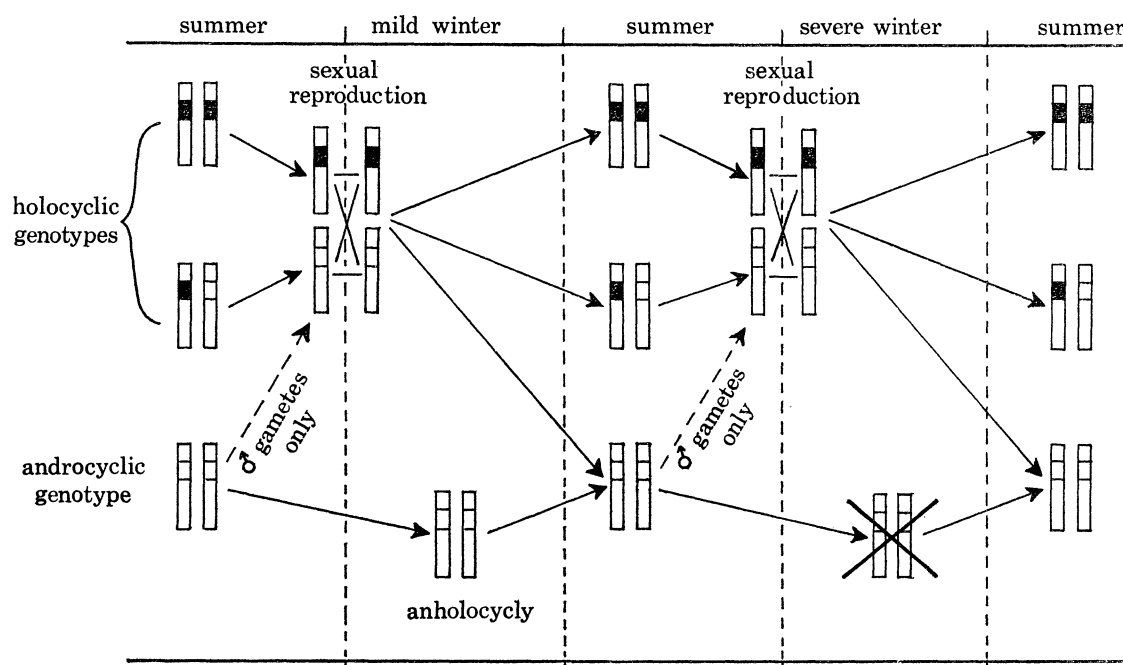

FIGURE 2. Maintenance of life cycle variation in *Myzus persicae* through three seasons. Androcyclic clones are generated afresh by the breeding system each year, even after a severe winter when parthenogenetic morphs outdoors are eliminated.

In Britain, the only truly anholocyclic *M. persicae*, with no response at all to short photoperiod, that have been found so far are of a characteristic dark green colour, and differ cytologically from the normal form of the species (Blackman 1971b). The differences appear to be due to simple fragmentation of one or two chromosomes of the normal complement (figure 3). Recently, another chromosomal variant of *M. persicae* has been found to occur commonly in glasshouses, in clones of androcyclic character (Blackman 1975, in preparation). This variant seems to be the result of a reciprocal translocation between two autosomes (figure 3d), and is frequently but not invariably associated with resistance to organophosphorus insecticides. The highly resistant form of *M. persicae* on chrysanthemums (Wyatt 1966) has this translocation. A similar or identical translocation heterozygote has now been found to occur commonly in Japan, where it is found in holocyclic as well as androcyclic clones, so that it must be incorporated into the breeding system. It is evident that the cytogenetics of *M. persicae* will repay further study.

HOST PLANT RELATIONS

British workers have been rather active in the study of the aphid–host plant relationship, and significant progress has been made in recent years. There have recently been a spate of review papers on different aspects of the subject. Eastop (1973b) discussed the evolution and specificity of aphid–plant relationships; Pollard (1973) comprehensively reviewed the mechanisms of

aphid feeding; Kennedy & Fosbrooke (1973) considered two aspects, the physiology of phloem sap feeding and the flight between host plants; Lowe & Russell (1975) covered host plant resistance to aphids with special reference to *M. persicae*; van Emden (1972, 1973, 1975) has summarized the whole field of aphid–host plant relations. It seems most useful here to select certain points which emphasize the practical implications of recent findings.
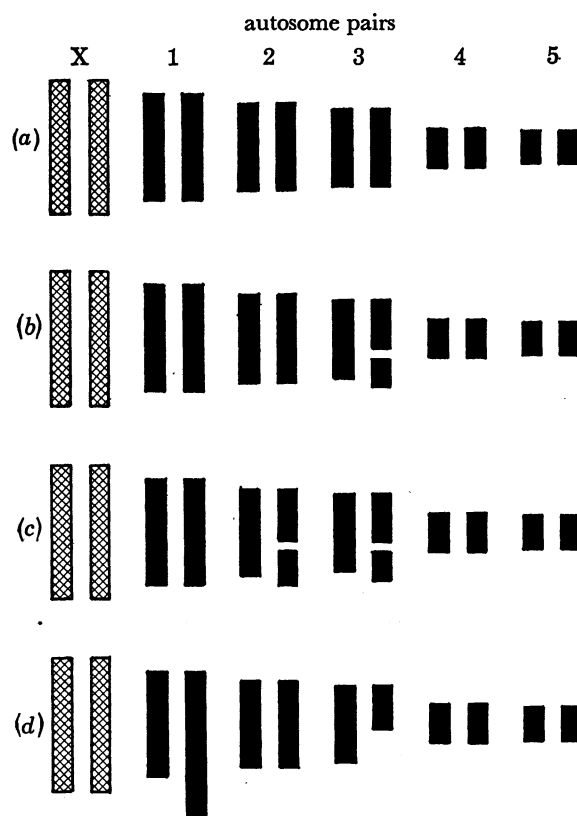

FIGURE 3. Chromosomal variation in *Myzus persicae*. Chromosomes arranged to fit the simplest hypothesis in each case. (*a*) normal karyotype ($2n = 12$); (*b*) one-break form ($2n = 13$); (*c*) two-break form ($2n = 14$); (*d*) karyotype with translocation between autosomes 1 and 3 ($2n = 12$).

M. persicae is probably the most polyphagous of all aphids, yet it has not been recorded from even 1 % of all vascular plants (Eastop 1973 *b*). The great majority of plants are apparently unsuitable for colonization. This is worthy of emphasis since polyphagy is often synonymized with a total absence of specificity. At Reading, van Emden & Bashford (1969, 1971) have shown that *M. persicae* is particularly sensitive to the physiological condition of those plants which it does colonize, if compared with an oligophagous species such as the cabbage aphid *Brevicoryne brassicae* (L.). This sensitivity may be manifested both in the selection of the plant or part of the plant that is colonized, and in the subsequent performance of the aphid. *M. persicae* selects artificial diets with optimum concentrations of sucrose and amino acids, and on living Brussels sprout plants prefers the old, senescing leaves on which it reproduces fastest (van Emden & Bashford 1969). When whole leaves of Brussels sprout were analysed for total soluble nitrogen, it was found that the old leaves contained less available nitrogen than young or mature leaves. However, the aphids feed from the phloem, which in senescing leaves is almost certainly a rich source of nutrients.

Comparison with *B. brassicae* is interesting and informative. *B. brassicae* colonizes the young parts of sprout plants preferentially where the concentration of mustard oil (sinigrin) is almost twice as high as elsewhere in the plant. Sinigrin acts as a phagostimulant for *B. brassicae* in artificial diets, whereas at high concentrations it may be repellent to *M. persicae*. Thus the results of laboratory work with artificial diets and with living plant material provide a very satisfactory explanation of the distribution adopted by the two aphid species on Brussels sprout plants (van Emden 1972).
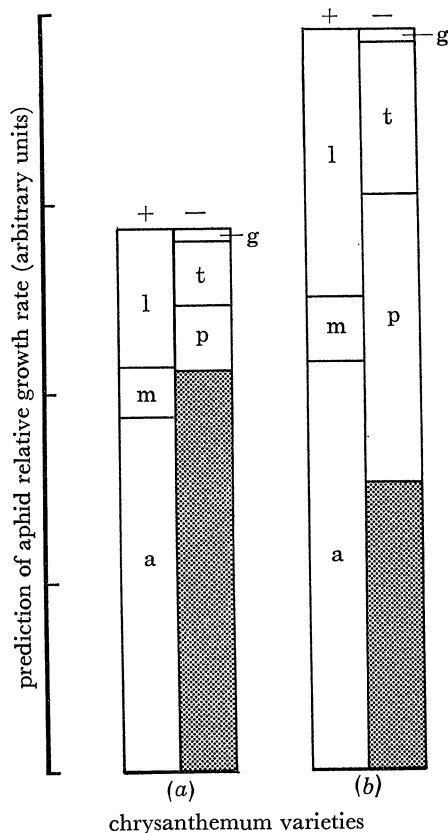

FIGURE 4. Prediction of the growth rate of *Myzus persicae* (shaded blocks) on two chrysanthemum varieties ((*a*) more susceptible than (*b*)), showing the contribution of: a, amide; g, γ-aminobutyric acid; l, leucine; m, methionine; t, tyrosine; p, proline. (From van Emden 1972.)

It is not the total amount of nitrogen available that is important to the aphids, but rather the quantities of particular amino acids. Van Emden & Bashford (1971) have shown that the growth rate of *M. persicae* is well correlated with the concentrations of certain amino acids in mature host leaves. Growth rate is correlated positively, for example, with increase of methionine. But it seems that negative correlations are just as important. The growth rate decreased, for example, with increasing concentrations of γ-amino butyric acid. In the case of *B. brassicae*, individual amino acids were implicated in the aphids' performance, but different ones. In fact, the amino acids which were important to *M. persicae* were those showing the greatest variation in concentration, which may explain why *M. persicae* is more responsive than *B. brassicae* to differences in the total amount of available nitrogen. Van Emden (1972) has used regressions of amino acid and mustard oil concentrations on aphid growth rate to devise models with which to predict the performance of the aphids on different varieties of a host plant. 'Un-

'favourable' amino acids which correlate negatively with performance seem to contribute greatly to the relative resistance of certain varieties, of chrysanthemum to *M. persicae* for example (figure 4).

The breeding of crop plants which carry a degree of resistance to aphids may be one way of reducing the need for chemical control (Lowe & Russell 1975), but the value of such resistance depends greatly on its continuing effectiveness. If resistance-breaking genes occur naturally in aphid populations, then it is better to know about them before embarking on an expensive and
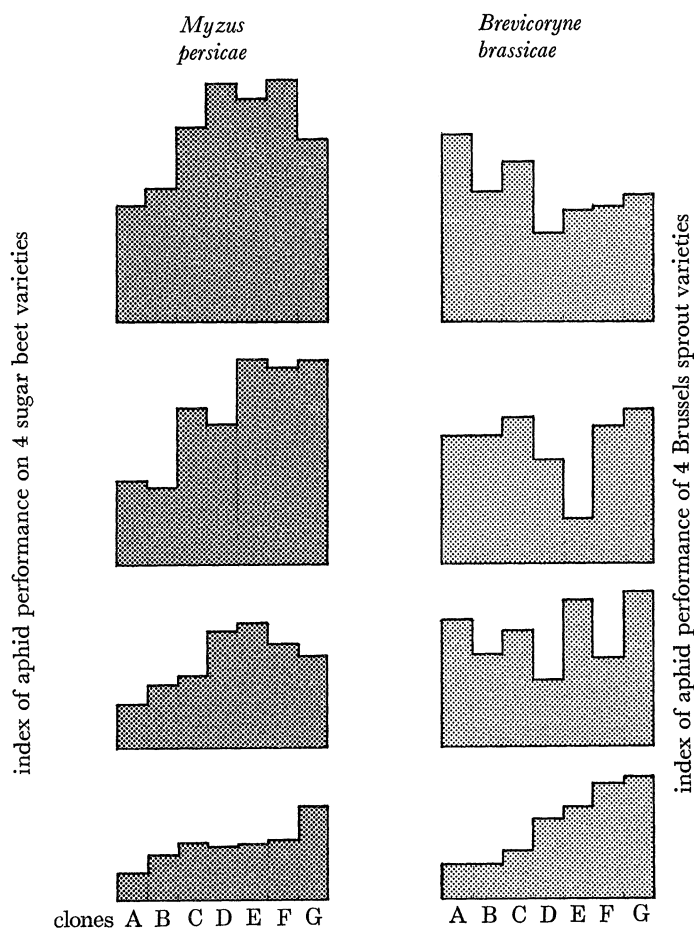

FIGURE 5. Comparison of plant/aphid genotype interactions of *Myzus persicae* and *Brevicoryne brassicae*. For each species, the reproductive performances of seven diverse genotypes are compared on four host plant varieties of differing susceptibility. *M. persicae* clones show consistent differences in vigour which are maintained on both resistant and susceptible varieties of sugar beet. Clones of *Brevicoryne brassicae* show no consistent pattern of response to Brussels sprout varieties. (Data from Lowe (1974) and Dunn & Kempton (1972).)

time-consuming programme of breeding for a level of crop resistance which may only last for one season. Working at the Plant Breeding Institute, Lowe & Russell (1969) showed that there is a considerable potential of inherited resistance to aphids in sugar beet. Lowe (1971, 1973, 1974*a*, *b*) has subsequently investigated the extent to which the performance of *M. persicae* varies on resistant beet stocks by studying a large number of aphid clones in the laboratory. Clones of *M. persicae* clearly differed in their vigour on, or their ability to colonize, sugar beet, but these differences were observed irrespective of whether or not the beet stock was resistant

(figure 5). Three unrelated beet stocks were consistently resistant, although infested by *M. persicae* from many sources.

The work of Dunn & Kempton (1972), who conducted a comparable investigation at Wellesbourne with *B. brassicae* on Brussels sprout, provides an almost startling contrast to Lowe's results. Sprout plants observed to be resistant to attack by *B. brassicae* in the field were clonally propagated and tested with cabbage aphids from different parts of England. Although seven sprout clones were consistently resistant to the cabbage aphids collected at Wellesbourne, the results with aphids collected in other localities were completely different, and only one sprout clone maintained any significant degree of resistance to all the aphids tested. The outlook for breeding resistance to cabbage aphid in Brussels sprout does not seem very bright. *B. brassicae* is a 'crucifer specialist' which appears to have developed specific preadaptations to cope with the genetic heterogeneity in its host plants. In the case of a polyphagous aphid such as *M. persicae*, however, there is probably inadequate selection pressure for the development of such specializations with respect to any particular host plants.

The validity of this statement may depend on the degree to which *M. persicae* has evolved genotypes with specific host plant associations. This is something we know very little about. Life cycle studies have in fact indicated a significant degree of specificity within the species to important crop host plants. When populations on adjacent brassica and potato crops were sampled and their reproductive category determined, the proportion of androcyclic genotypes was far greater (92 %) on brassicas than on potatoes (39 %) (Blackman 1975). As androcyclic genotypes can pass the winter on certain brassica crops but not on potatoes, linkage between this life cycle trait and a predilection for brassicas as host plants would seem to be advantageous to the species. However, clearly defined host-specific 'races' are only likely to occur as a result of reproductive isolation, as, for example, when the sexual phase is lost completely. Anholocyclic 'races' so formed may be capable of some genetic change by mutation, and possibly by a mechanism of endomeiotic recombination, but their potential responses to variation in the host plant must be severely limited in comparison with the sexually reproducing species. Therefore it still seems justifiable to conclude that the more polyphagous aphids are the least likely to develop resistance-breaking genotypes.

Work with resistant plant varieties has tended to confirm conclusions gained with artificial diets, that aphids select plants on which they can perform best, so that non-preference and antibiosis often go together and resistant plants are less likely to be colonized by immigrant alatae. Thus, resistance to the aphid can provide a level of protection against virus transmission as well as against colonization and direct aphid damage, especially if resistance to the virus itself can also be incorporated into the crop. Although *M. persicae* is most important as a virus vector, van Emden (1975) has reported that aphids can cause a striking reduction in root dry mass, coupled with increased respiration, of Brussels sprout plants merely by their probing and salivation, continued feeding being prevented. It seems that even the sparse populations of *M. persicae* on most crops may cause direct damage and affect plant growth and yield more than is readily apparent. Dixon (1971*a*, *b*) has demonstrated comparable physiological effects of certain Callaphidine aphids on trees, which form relatively sparse populations but nevertheless significantly reduce growth and wood formation.

Population dynamics

From the outset of the I.B.P. aphid project, one of its primary objectives has been a concentrated, international effort to study the population ecology of *M. persicae*. G. N. Foster has acted as the coordinator of this study, with the help of H. F. van Emden. The very considerable problems involved in ecological studies of a pest aphid have already been mentioned. The idea was to concentrate attention on populations of *M. persicae* on one secondary host plant, potato, and to conduct strictly comparable studies of the dynamics of such populations simultaneously in as many parts of the world as possible. It was hoped that this approach would provide sufficient quantitative data about the development of *M. persicae* populations, and the influence of the various natural control factors, to enable some generalizations to be made, which would apply at least to this particular aphid-crop association, and could also serve as a model for future work on other aphids and other host plants.

An appropriate ecological method was required which would enable the essential data to be collected by a fairly simple procedure with a minimum of manpower and resources. Aphids have overlapping generations, for which the most widely used methods of population study are inapplicable. Fortunately, a very appropriate technique was developed by Hughes (1963) for the cabbage aphid in Australia. Hughes (1972) has reviewed the application of his method to aphids in general. Briefly, the two main concepts involved are the *physiological time-scale* and the *time-specific life-table*. The physiological time-scale (a scale of accumulated day-degrees above a certain threshold temperature) enables numerical changes which occur at different or fluctuating temperatures to be compared directly. With aphids, the larval instars are approximately equal in duration on such a scale, so that the *instar period* of a species is a constant number of day-degrees and can be used as a biologically meaningful unit. Time-specific life tables were originally developed for actuarial purposes, overlapping generations being one property that is common to both human and aphid populations. They are used to describe numerical changes in a population during a given short interval of time, which in aphids is conveniently one instar period.

The procedure is to take two samples from a population which will provide estimates of the population density one instar period apart (a 'twin sample'). Provided that the age structure of the population is stable, the numbers of individuals in each instar in the first sample can be used to estimate the potential increase of the population over one instar period (figure 6). The density predicted from the first sample is then compared with the observed density obtained from the second sample, the difference between predicted and observed values providing an estimate of the losses from the population over one instar period. Some part of the losses can be accounted for. Mortality due to parasitism and disease, for example, can be estimated by holding some aphids for one instar period in the laboratory, and losses due to emigration of winged aphids from the population can be calculated from the number of fourth instar nymphs with wing buds in the first sample. Unfortunately, predation cannot be estimated directly, but is generally assumed to be a major part of any remaining difference. Separate field studies of predator abundance and activity are necessary to decide to what extent this interpretation of the residual mortality is correct.

All participants in the population dynamics project were provided with a technical manual detailing the procedures involved and including a key to the identification of the larval instars of *M. persicae*. It was suggested that twin samples should be taken three times during the season:

(i) during the period of exponential growth of the population about 300 day-degrees after *M. persicae* was first detected on the crop, (ii) as the population approached its peak density, and (iii) during the initial part of the population decline. The field experiment was taken up by 16 workers in ten countries, and 13 sets of 'twin sample' data were obtained from eight participants in five countries, covering the northern hemisphere from 37 to 56° N. This response did not completely fulfil expectations, but nevertheless the results showed a high degree of consistency, and enabled some valuable general conclusions to be drawn about the factors influencing populations of *M. persicae* on potato (Foster & van Emden 1975). Figure 6 illustrates the results of a fairly typical twin sample. Losses due to parasitism and disease were invariably very small, especially before the population peak. Emigration generally comprised a steady departure of relatively few individuals from just before peak density until the end of the season. *M. persicae* is probably an atypical aphid in this respect, as it does not form aggregates on its secondary host plants. The interaction between individuals in many aphid species which form crowded populations can result in production of a high proportion of alate individuals at or around the population peak.
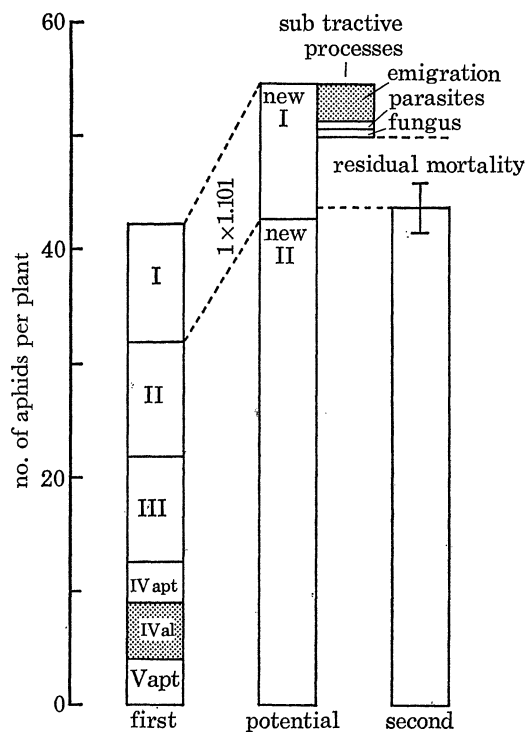

FIGURE 6. Example of a time-specific analysis of a *Myzus persicae* population from twin-sample data.

The residual mortality, which includes the losses due to predation, was high in almost all sets of data. High residual mortality could only be confidently ascribed to predation where complementary studies showed that predators were active or abundant, but it did appear that predators were important in limiting numbers of *M. persicae* in several diverse areas. High mortality often occurred well before the population peak, although it was invariably at its maximum level after the peak when the specifically aphid-eating insects such as coccinellids and syrphids had had a chance to build up their numbers. Early-season mortality was sometimes attributable to non-specific predators of the ground fauna (see, for example, Foster 1972).

An important conclusion was that predators are unlikely to be the direct cause of the decline of a *M. persicae* population unless the aphids are increasing at well below their maximum rate. Quite high rates of predation can fail to control aphid populations which are reproducing at a moderate rate. Potato is in fact a relatively poor host for *M. persicae*, so that aphid increase rates in the study were generally rather low. On other host plants such as tobacco the aphids' increase rate may be too high for predators to ever have any impact before the population peak. This conclusion does, however, once again highlight the important influence of host plant species and condition on the build-up of aphid populations, especially when the aphid is a polyphagous species on a relatively unfavourable host plant (van Emden & Way 1973).

<div align="center">DISPERSAL BY FLIGHT</div>

The most problematical aspect of aphid ecology is undoubtedly the study of migration and dispersal between host plants. No matter how much can be achieved in the way of elucidating the ecology of aphid populations on particular crop or other host plants, it seems likely that the high and largely unpredictable mortality of the migratory phase will defeat any attempt to devise a quantitative, predictive model of the total life system.

Nevertheless, even if we have to be satisfied with something less than an understanding of the complete life system, we need to know a great deal more about aphid migration and dispersal in order to devise and operate efficient control practices. Taylor (1974a) emphasizes the importance of the spatial element in the ecology of crop pest insects. Changes in distribution may have more bearing on practical control problems than changes in number. This is obviously true of a polyphagous nomad such as *M. persicae*. The whole pattern of distribution over large areas of land may alter in a matter of days. How then can the total population of such an aphid species be monitored on a national or even international scale, quickly and accurately enough to follow these distributional changes? Ten years ago this seemed an insuperable problem. Now the Rothamsted Insect Survey, developed largely through the efforts of L. R. Taylor, seems to be providing the answer, while at the same time opening up a whole new field of aphid population studies.

The Rothamsted Insect Survey samples a constant volume of air for flying aphids and other small insects by means of a nationwide system of suction traps. Technical aspects are discussed by Taylor & Palmer (1972). An essential point is that the air is sampled at a fixed height (12.2 m) above ground where aphids and other small flying insects are effectively dispersed at random. Under these conditions there is a near-linear logarithmic relation between density and height (Taylor 1974b), so that when the density gradient is known the total number of aphids flying over a given area of ground can be estimated by integration. By 1973, the survey was operating 20 suction traps; 18 in Great Britain, one in Denmark and one in Holland. An aphid warning scheme has been in operation since 1968, issuing weekly bulletins which list the catches of 32 kinds of aphids. Since the suction traps have been in operation they have almost always recorded the initial spring migration of aphid pests to cereals (Taylor 1974a) and sugar beet (Heathcote, Palmer & Taylor 1969) before the first aphids were discovered on the crop. The greatest advantage of the suction trap forecasts, however, is that they circumvent laborious crop inspection routines and simultaneously cover many different aphid species and different crops.

It is with the advent of computer mapping techniques, however, that the full value and

potential of synoptic sampling methods for aphids and other insects in flight is being revealed (Taylor 1973, 1974a). Most important pest aphids such as *M. persicae* disperse so widely that relatively few suction traps are needed to build up the total picture of seasonal changes in distribution and provide estimates of population change over the whole of Britain. By totalling samples over a whole year to eliminate phenological complications, the annual blanket coverage of the country by alatae of such a species is demonstrated. Summation over shorter intervals of time reveals regional variations in the timing of migration, and the existence within any one year of several distinct population cycles crossing the country in waves (figure 7). Certain other species, including pests such as the damson-hop aphid *Phorodon humuli* (Schrank), show wide diffusion from a region of strong concentration in spring, when their distribution is restricted to that of their primary host plant. Both types of distributional pattern hold considerable prospects for further analysis and interpretation.
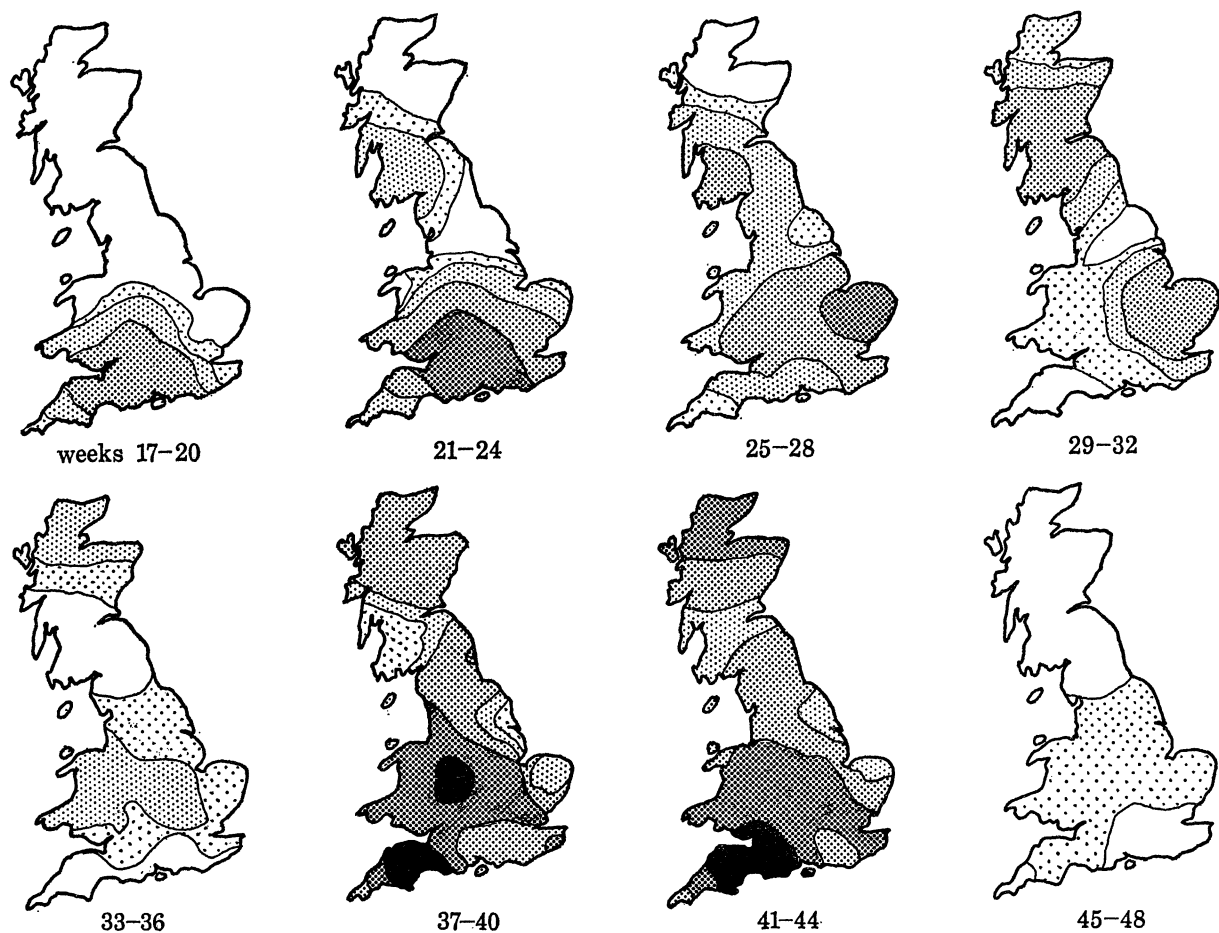

FIGURE 7. Aerial densities of *Myzus persicae* summed over 4 week periods for the season 1971, based on computer analysis of suction trap catches (after Taylor 1974).

Not all the problems of aerial sampling of aphids have been solved. Much more information on density gradients is required before total aerial populations can be estimated with confidence for all species at all times of year. A fundamental difficulty in predicting crop infestations is that the relationship between aphids in the air and aphids on the crop may be rather tenuous. Aphids are not deposited on the ground like inert particles but fly in the boundary layer before

alighting on plants. Alightment, whether or not on a suitable plant, is almost invariably followed by re-take-off. Behaviour will vary between and even within species, as well as being influenced by factors such as the climate in the boundary layer and the degree of resistance offered by the plant. Nevertheless, with continuous synoptic information about aerial aphid populations it should be possible to learn a great deal about the very important host finding and selection processes of aphids by studying the discrepancies between numbers in the air and numbers on the crop.

Conclusions

A wide range of research activities have been covered in this report. Before considering how they relate to the practical problems of devising rational pest control practices, I shall summarise as succinctly as possible some of the most important points to emerge from these studies.

(1) Work on life cycle variability in *M. persicae* exemplifies the need for a better understanding of the genetic basis of variation in aphids. Any new control measure exerts a pressure for genetic change on the pest population. A successful long-term strategy will have to take full account of not only the variation already manifested by aphids but also their hidden potentialities to respond genetically to new situations.

(2) Aphis species show considerable differences in their physiological relations with their host plants. The highly polyphagous *M. persicae* seems poorly adapted physiologically to some of its principal secondary host plants, so that the host plant species and condition may be factors of considerable importance in limiting its populations. Other less polyphagous aphids may be less sensitive to physiological differences in their host plants, or have greater genetic potential to adapt to such variation.

(3) Of the natural enemies of *M. persicae*, only predators have much impact on populations on potato, and these only cause a decline if they are present in large numbers early in the season, or when the aphids are increasing at well below their maximum rate.

Finally, two significant developments in methodology:

(4) The population dynamics project on *M. persicae* on potatoes has demonstrated the ability of Hughes' method of time-specific analysis to overcome many of the difficulties of studying aphid populations on their host plants and to provide meaningful data from which to assess the relative importance of the various natural control agencies. Hopefully, the more extensive use of this method with different aphid species in diverse situations will greatly add to our knowledge of aphid population ecology.

(5) The Rothamsted Insect Survey has not only shown how a system of suction traps can simultaneously provide an efficient warning service for many aphid pests on different crops, but has also started to clarify our very hazy ideas about what happens to aphids in their migration and dispersal phase between host plants. If the method were adopted internationally it could soon be possible to trace aphid movements on a continental scale.

M. persicae occurs on a wide variety of crops in many different situations, each requiring the development of a separate control strategy. The results of I.B.P. work on aphids suggest that the 'Achilles heel' of *M. persicae* may be its sensitivity to the physiological condition of its host plant. In the completely artificial glasshouse environment, Wyatt (1970) has shown that the parasite *Aphidius matricariae* is more likely to check *M. persicae* on resistant varieties of chrysanthemum than on susceptible ones. A system of integrated control has now been devised at the Glasshouse Crops Research Institute for *M. persicae* on glasshouse chrysanthemums (Scopes

1970; Scopes & Biggerstaff 1973), which combines introductions of *A. matricariae* with the use of resistant chrysanthemum cultivars and occasional applications of a selective insecticide. In the field crop situation, a more complex interplay of factors must be considered. Breeding for only moderate levels of resistance in the crop plant, or altering the plant's physiology by the use of fertilizers (van Emden 1966) or plant growth regulators (van Emden 1969), could greatly affect colonization and development of *M. persicae* populations and provide the best foundation for an integrated control strategy. A low level of 'non-specific' host plant resistance to aphid attack, based on several independent mechanisms and controlled by many genes as in sugar beet (Lowe & Russell 1969), may be more valuable for lasting control than single-gene resistance, which although possible highly effective in the short term could be broken more easily by the aphid. In the immediate future, carefully timed applications of selective chemicals and enhancement of the effect of predators by providing them with alternative food supplies early in the season seem to be the most logical and widely applicable supporting measures. Cultural practices, such as those helping to prevent virus spread, will be important in particular cases. To achieve any degree of permanence, the control of aphids such as *M. persicae* must be approached on as broad a front as possible with each step based on sound ecological knowledge.

References (Blackman)

Blackman, R. L. 1971 *a* Variation in the photoperiodic response within natural populations of *Myzus persicae* (Sulzer). *Bull. ent. Res.* **60**, 533–546.

Blackman, R. L. 1971 *b* Chromosomal abnormalities in an anholocyclic biotype of *Myzus persicae* (Sulzer). *Experientia* **27**, 704–706.

Blackman, R. L. 1972 The inheritance of life-cycle differences in *Myzus persicae* (Sulzer). *Bull. ent. Res.* **62**, 281–294.

Blackman, R. L. 1974 Life-cycle variation of *Myzus persicae* (Sulzer) in different parts of the world, in relation to genotype and environment. *Bull. ent. Res.* **63**, 595–607.

Blackman, R. L. 1976 Life-cycle variations. In *Studies in biological control* (ed. V. Delucchi), *IBP Synthesis report* no. 9. Cambridge University Press.

Dixon, A. F. G. 1971 *a* The role of aphids in wood formation. I. The effect of the sycamore aphid *Drepanosiphum platanoides* (Schr.) on the growth of sycamore, *Acer pseudoplatanus* L. *J. appl. Ecol.* **8**, 165–179.

Dixon, A. F. G. 1971 *b* The role of aphids in wood formation. II. The effect of the lime aphid *Eucallipterus tiliae* L. on the growth of the lime, *Tilia × vulgaris* Hayne. *J. appl. Ecol.* **8**, 393–399.

Dunn, J. A. & Kempton, D. P. H. 1972 Resistance to attack by *Brevicoryne brassicae* among plants of Brussels sprouts. *Ann. appl. Biol.* **72**, 1–11.

Eastop, V. F. 1973 *a* Biotypes of aphids. In *Perspectives in aphid biology* (ed. A. D. Lowe), pp. 40–51. *Bull. ent. Soc. N.Z.* **2**.

Eastop, V. F. 1973 *b* Deductions from the present day host plants of aphids and related insects. In *Insect/Plant Relationships. Symp. R. ent. Soc. Lond.* **6**, 157–178.

van Emden, H. F. 1966 Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* on Brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomologia exp. appl.* **9**, 444–460.

van Emden, H. F. 1969 Plant resistance to *Myzus persicae* induced by a plant regulator and measured by aphid relative growth rate. *Entomologia exp. appl.* **12**, 125–131.

van Emden, H. F. 1972 Aphids as phytochemists. In *Phytochemical ecology* (ed. J. B. Harborne), *Phytochem. Soc. Symp. Series* No. 8. London: Academic Press.

van Emden, H. F. 1973 Aphid-host plant relationships. Some recent studies. In *Perspectives in aphid biology* (ed. A. D. Lowe), pp. 54–64. *Bull. ent. Soc. N.Z.* **2**.

van Emden, H. F. 1976 Host plant interactions. In *Studies in biochemical control* (ed. V. Delucchi) *IBP Synthesis report* no. 9. Cambridge University Press.

van Emden, H. F. & Bashford, M. A. 1969 A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. *Entomologia exp. appl.* **12**, 351–364.

van Emden, H. F. & Bashford, M. A. 1971 The performance of *Brevicoryne brassicae* and *Myzus persicae* in relation to plant age and leaf amino acids. *Entomologia exp. appl.* **14**, 349–360.

van Emden, H. F., Eastop, V. F., Hughes, R. D. & Way, M. J. 1969 The ecology of *Myzus persicae*. *A. Rev. Ent.* **14**, 197–270.

van Emden, H. F. & Way, M. J. 1973 Host plants in the population dynamics of insects. In *Insect/plant relationships. Symp. R. ent. Soc. Lond.* **6**, 181–199.

Foster, G. N. 1972 The population dynamics of aphids infesting potato. Ph.D. Thesis, University of Newcastle-upon-Tyne.

Foster, G. N. & van Emden, H. F. 1976 Population dynamics on potatoes. In *Studies in biological control* (ed. V. Delucchi), *IBP Synthesis Report* no. 9. Cambridge University Press.

Heathcote, G. D., Palmer, J. M. P. & Taylor, L. R. 1969 Sampling for aphids by traps and by crop inspection. *Ann. appl. Biol.* **63**, 155–166.

Hughes, R. D. 1963 Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.). *J. anim. Ecol.* **32**, 393–424.

Hughes, R. D. 1972 Population dynamics. In *Aphid technology* (ed. H. F. van Emden), pp. 275–293. London: Academic Press.

Hull, R. 1974 Integrated control of pests and diseases of sugar beet. In *Biology in pest and disease control* (ed. D. Price Jones & M. E. Solomon), pp. 269–276. Oxford: Blackwell.

Kennedy, J. S. & Fosbrooke, I. H. M. 1973 The plant in the life of an aphid. In *Insect/plant relationships. Symp. R. ent. Soc. Lond.* **6**, 129–140.

Lowe, H. J. B. 1971 The role of varieties in controlling pests and diseases. *I.I.R.B.* **5**, 224–231.

Lowe, H. J. B. 1973 Variation in *Myzus persicae* (Sulz.) reared on different host plants. *Bull. ent. Res.* **62**, 549–556.

Lowe, H. J. B. 1974*a* Testing sugar beet for aphid-resistance in the glasshouse: a method and some limiting factors. *Z. ang. Ent.* **76**, 311–321.

Lowe, H. J. B. 1974*b* Intraspecific variation in *Myzus persicae* (Sulz.) on sugar beet (*Beta vulgaris* L.). *Ann. appl. Biol.* **78**, 15–26.

Lowe, H. J. B. & Russell, G. E. 1969 Inherited resistance of sugar beet to aphid colonisation. *Ann. appl. Biol.* **63**, 337–343.

Lowe, H. J. B. & Russell, G. E. 1976 Breeding plants for aphid-resistance. In *Studies in biological control* (ed. V. Delucchi), *IBP Synthesis Report* no. 9. Cambridge University Press.

Needham, P. H. & Devonshire, A. L. 1975 Resistance to some organophosphorus insecticides in field populations of *Myzus persicae* from sugar beet. *Pest. Sci.* (In the Press.)

Pollard, D. G. 1973 Plant penetration by feeding aphids: a review. *Bull. ent. Res.* **62**, 631–714.

Scopes, N. E. A. 1970 Control of *Myzus persicae* on year-round chrysanthemums by introducing aphids parasitized by *Aphidius matricariae* into boxes of rooted cuttings. *Ann. appl. Biol.* **66**, 323–327.

Scopes, N. E. A. & Biggerstaff, S. M. 1973 Progress towards integrated pest control on year-round chrysanthemums. *Proc. 7th Br. Insecticide & Fungicide Conf.* **1**, 227–233.

Taylor, L. R. 1973 Monitor surveying for migrant insect pests. *Outlook on Agriculture* **7**, 109–116.

Taylor, L. R. 1974*a* Monitoring changes in the distribution and abundance of insects. *Rep. Rothamsted exp. Stn* **1973** (2), 202–239.

Taylor, L. R. 1974*b* Insect migration, flight periodicity and the boundary layer. *J. Anim. Ecol.* **43**, 225–238.

Taylor, L. R. & Palmer, J. M. P. 1972 Aerial sampling. In *Aphid technology* (ed. H. F. van Emden), pp. 189–234. London: Academic Press.

Wyatt, I. J. 1966 Insecticide resistance in aphids on chrysanthemums. *Proc. 3rd Br. Insecticide & Fungicide Conf.* 1965, 52–55.

Wyatt, I. J. 1970 The distribution of *Myzus persicae* (Sulz.) on year-round chrysanthemums. II. Winter season: the effect of parasitism by *Aphidius matricariae* Hal. *Ann. appl. Biol.* **65**, 31–41.